Aerodynamic Aspects of Animal Flight

Gauß Lecture 1975

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by
Sir James Lighthill

From this Gauß Lecture we print here only Part 3 which describes the newest material. The Institute of Mathematics and its Applications (address: Maitland House, Warrior Square, Southend-on-Sea, Essex, England) has published in the October 1974 issue of its Bulletin the whole lecture. Its scope is indicated by the following Table of Contents, and by the Bibliography at the end of the present text.

Hovering Flight, Take-off and Landing

3.1 Normal

After discussing many different aspects of sustained forward flight in part 2, now I want to describe hovering flight: movements of wings through which the *body* of an animal remains effectively motionless *in still air*. This fascinating subject must not be neglected altogether in a lecture on 'Aerodynamic Aspects of Animal Flight'.

A capacity for sustained hovering flight is characteristic above all of the flying *insects*. We may observe that many of their modes of life, and especially their very successful symbiosis with the flowering plants noted in section 1.2, make great use of this capacity. It is facilitated, furthermore, by their range of *sizes*, since the upper limit on size for animals capable of sustained flight, noted in section 2.7, is reduced enormously if the animal's weight must be supported *without* the aid of any horizontal relative wind. Indeed, among birds and bats sustained hovering in this sense is possible only in

certain animals at the low end of the size range, outstanding examples being the hummingbirds (Trochilidae) with masses at *most* 20g (found in *Patagona gigas*), or small bats with masses around 10g. The largest hovering insects like the elephant dung beetle *Heliocopris* are in the same size range 10 to 20g.

There is obviously great interest, both in observing the wing motions whereby flying animals with masses around 10 to 20g or less can hover in still air for extended periods, and in studying how aerodynamic, skeletal and muscular limitations may have combined to set this upper limit to the mass of such animals. Yet another excellent reason for studying the *same* wing motions is that much larger flying animals are commonly capable of making them *for short periods*, using the characteristic ability of muscle to generate anaerobically, for such short periods, much greater powers than can be sustained continuously under limitations imposed by oxygen supply.

Those larger flying animals, which can briefly make the motions of hovering flight to support their weight in still air, use that ability especially in take-off and landing. In aeronautical terms they are 'V.T.O.L.'; for example, they take off vertically by making 'hovering' movements, followed as quickly as possible by a transition to ordinary forward flight (see below). These, indeed, are the commonest take-off arrangements in birds, the principal exceptions having been noted in section 2.3 (take-off under gravity from elevated positions) and section 2.7 (runway-type take-off, especially found in aquatic birds).

In his general review of sustained hovering flight, Weis-Fogh (1973) has identified an essentially common pattern of what he has named 'normal hovering' in the hummingbirds generally (Trochilidae) and in insects from eleven different orders. These motions of 'normal hovering' may be recognised as an adaptation of those flapping motions that are used for forward flight. Lift for weight support requires horizontal movements of wings relative to the air: therefore, in the absence of any horizontal movement of the animal as a whole relative to the air, the wings must themselves beat *horizontally* back and forth. Evidently wings, that for forward-flight purposes beat in a plane perpendicular to the horizontal body axis, are readily adapted to this requirement if the body axis becomes erect (that is, practically vertical) in hovering flight.

Figure 50 depicts normal hovering flight in the sphingid moth *Manduca sexta* viewed from above. As just suggested, the body axis is practically vertical, which facilitates beating of the wings in an approximately horizontal plane. In order to ensure that the wing leading edge moves forward always at an effective angle of attack within the range for good lift-drag ratio, the twisting movements are necessarily much enhanced: the usual pronation at the start of the downstroke is greatly intensified (frames (a) and (b)), leading to a horizontal wing movement (frames (c) to (g)) with the upper surface uppermost at a geometrical angle of attack of less than 30°. (The effective angle of attack is still smaller because the wings move in the general downdraught produced by the animal's hovering activity.) Next, the usual supination at the start of the upstroke is greatly intensified (frames (h) and (i)), so that the wing with its *underside* uppermost (and thus with the *same* leading edge leading!) follows in reverse the previous horizontal path at approximately the same angle of attack. Both strokes generate the lift needed to support the animal's weight.

Figure 51, depicting the path of the wing tip during the sustained hovering of a hummingbird (Stolpe & Zimmer 1939), demonstrates that essentially the same motions, which Weis-Fogh calls those of 'normal hovering flight', are used. Figure 52 reminds us that many hummingbirds have 'converged' with insects not only in their flying motions but also in their ways of life; the lower photograph, indeed, shows one not much larger than a bumblebee. Compared with the insects, they have the advantage of high lift coefficients C_L (about 2·0 according to Weis-Fogh's estimates) resulting from the properties of wings with feathers which in flash photographs like figure 52 are shown to be spread in a lift-enhancing manner. On the other hand, they lack the insects' elastic systems. Even with their high C_L, they need to beat their wings at high frequencies (15 to 50 Hz) to support their weight, and the associated power requirements (Weis-Fogh 1972) are not far below the maximum values indicated in section 2.7 (although an elastic system would have reduced them by 40%).

We have observed that 'normal hovering' is a rather logical adaptation to hovering requirements of the wing capabilities needed in flapping forward flight. An actual *transition* between the two modes is interesting to watch in large birds as they come in to land. Figure 53 is from an old film record of a gull alighting (Horton-Smith 1938) which makes the sequence clear enough. First the tail feathers are spread, feet dropped and wings arched to provide braking while the body becomes more erect, the stroke plane of the wing-beat turns from vertical to horizontal and the twistings of the wing are intensified; finally, as the bird alights, its weight is being supported by the lift on horizontally moving wings.

In take-off, again, a few strong strokes of 'normal hovering' with the body almost erect are followed by a transitional 'slow forward flight' mode of motion (Brown 1948) which is an interesting blend of the motions of normal hovering and of fast forward flight, with an intermediate degree of wing twisting at the extremes of the stroke (figure 54). The stroke plane is diagonal so that even at a low forward speed the wings can develop both thrust and lift without stalling. By comparison with *pure* hovering, however, the power needed for weight support is much *reduced*, because the wing's component of forward motion relative to the body in the heavily loaded downstroke can effectively be lessened by about the speed of the body's forward motion through the air.

There are those who assert that the kestrel *Falco tinnunculus* is capable of sustained hovering motions in still air. Aerodynamically, it would be surprising if this bird with typical mass 200 g, an order of magnitude greater than the largest hummingbird, could support its weight in still air for long periods by motions compatible with its muscular and skeletal limitations. Furthermore, it is not always recognised that, in those open places where kestrels are seen motionless in the air, there is normally a significant horizontal wind component. Ornithologists of great experience have stated that the kestrel remains motionless *only* under those conditions, facing into the wind (see for example Witherby 1939, p. 26); and the wing motions they describe are precisely those of slow forward flight (figure 54), which could presumably maintain the bird stationary in a modest wind without impossible metabolic or structural demands.

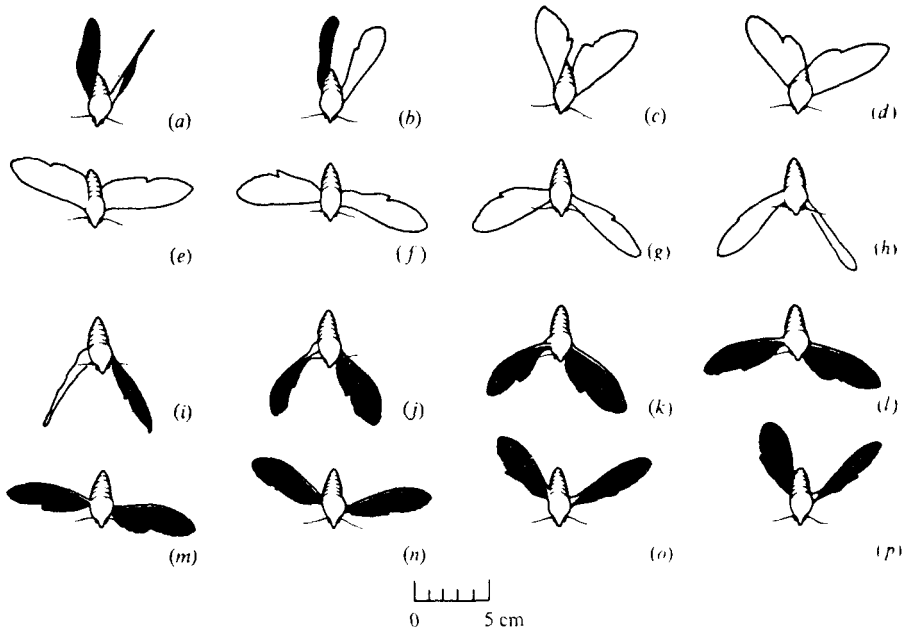

Figure 50.
Normal hovering of Manduca sexta as traced from a slow-motion film, with the undersides of the wings shaded black (Weis-Fogh 1973).

3.2 Exceptional

Weis-Fogh (1973), while establishing that the hovering motions described in section 3.1 are found so very widely that they can properly be designated as those of 'normal' hovering flight, identified also certain groups of animals exceptional in the types of motion used. These all raise aerodynamic questions of very considerable interest.

We have implied that the size range for hovering animals is limited at its upper end by a conflict between the maximum lift coefficient that can be achieved (which defines the speeds of horizontal wing motions required for weight support) and the animal's muscular and skeletal limitations. On the other hand, these latter limitations conflict with a *different* aerodynamic requirement at the lower end of the size range. Lift generation by classical horizontal motion of an aerofoil at an appropriate angle of incidence becomes less and less effective as the Reynolds number Uc/ν based on aerofoil velocity U and chord c falls to very low values: say, below 50 (Thom & Swart 1940). Then, thick boundary layers bring about poor lift-drag ratios, as well as severe difficulties in generating adequate circulation for lift purposes by the usual processes of trailing-edge vortex shedding. 'Normal' hovering requires two reversals of circulation per wing beat, and lags in achieving these can be expected to be enhanced at very low Reynolds numbers.

At the lower end of the range of sizes of insects capable of hovering, there are major problems in achieving Reynolds number high enough to avoid these difficulties. A lower limit on Reynolds number defines a lower limit on the wing speed U which *increases* (like l^{-1}) as an animal's linear dimension decreases. This means a lower limit on frequency increasing *very fast* (like l^{-2}), which for small enough insects again conflicts with upper limits imposed by structural and metabolic requirements.

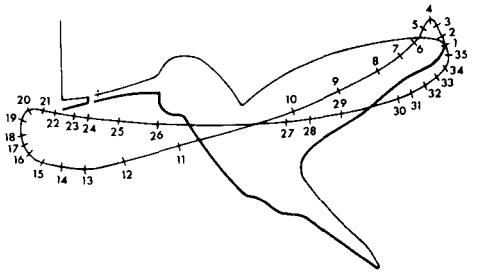

Figure 51.
Path of the wing tip of a hovering hummingbird (Stolpe & Zimmer 1939).

Figure 52.
Flash photographs of hummingbirds hovering near flowers (Scheithauer 1967).
Above: Lesbia victoriae.
Below: Calothorax lucifer.

Figure 53.
Phases in the landing of a gull (Horton-Smith 1938).

To be sure, the evolutionary opportunities for insects that could remain functionally effective at greatly reduced sizes gave rise, as has long been recognised (section 2.2), to remarkable muscular developments allowing the beating of wings at extraordinarily high frequenties. Now Weis-Fogh (1973) has shown that the same evolutionary opportunicies gave rise to aerodynamically novel modes of flight, permitting weight support at *lower Reynolds numbers* than would be possible with 'normal' hovering.

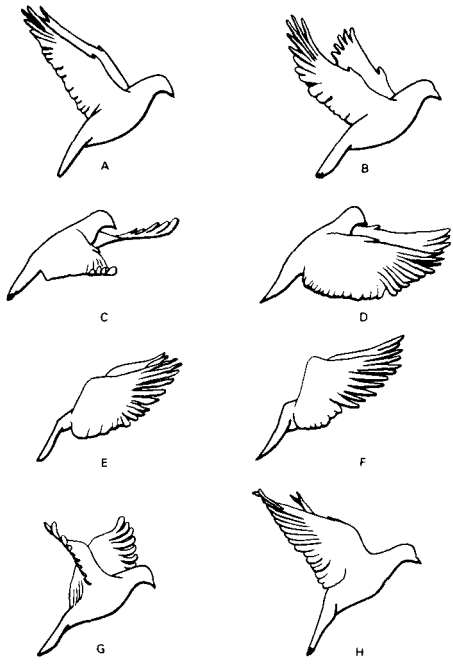

Figure 54.
Eight successive positions (A to H) in the slow forward flight of a pigeon (Brown 1948).

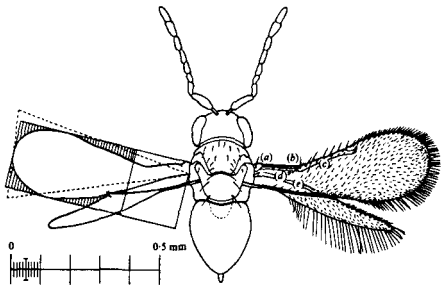

Figure 55.
Morphology of Encarsia formosa (Weis-Fogh 1973).

Figure 55 shows *Encarsia formosa*, an insect of size around 1 mm from the suborder Chalcidoidea of the Hymenoptera, on which Weis-Fogh did all the initial work of identifying these aerodynamically novel motions and demonstrating their significance. The two pairs of wings, being 'jugate' move effectively as a single pair. The wing-beat frequency, though as high as 400 Hz, yields a Reynolds number of only 20 in such a small animal: a value seemingly too low for generation of the lift needed for weight support. Indeed, Weis-Fogh showed from his observations that *Encarsia* requires a mean lift coefficient around 3, more than twice the maximum found at that Reynolds number in steady-state aerodynamics (Thom & Swart 1940); while the usual unsteady effects such as the 'Wagner effect' are known to imply a reduction from the steady-state figure.

Weis-Fogh went on to prove experimentally and theoretically, however, that the animal uses special unsteady effects, previously unknown to aerodynamicists: the 'clap and fling' mechanism of lift generation. He explained clearly how the 'clap and fling' manoeuvre, performed once per wing beat, generates immediately the circulation required for achieving a high lift coefficient without the need to wait for the classical processes of trailing-vortex shedding. Lighthill (1973b) analysed from an aerodynamical standpoint various features contributing to make this Weis-Fogh mechanism of lift generation so effective.

Professor Weis-Fogh's remarkable slow-motion pictures of the hovering motion of *Encarsia formosa,* taken at over 7000 frames per second, show what a considerably complicated wing-beat cycle this insect succeeds in performing 400 times a second. Figure 56 shows tracings from successive frames of that film. Note again the erect body of the insect during hovering; note also the positions of the legs which indicate that in these pictures the right-hand side, where the insect claps its wings, is the *dorsal* side of the insect's erect body.

The sequence begins (frames 15 and 0) with the wings temporarily at rest in the clapped-together position. The 'fling' then occurs (frames 1 and 2): a rapid rotation of the *effectively single pair of wings* (see above) *about a common axis along their trailing edges.* The rest of the motion (frames 3 to 13) is as in 'normal hovering' until the next 'clap' occurs (frames 14 to 16).

For a detailed analysis of these motions, see the papers cited. Briefly, the mechanism depends on the inrush of air into the opening gap between the wings during the 'fling' motion generating immediately about each wing a circulation of the right magnitude and sign to produce a high lift coefficient during the immediately ensuing stroke (without *any* conflict with Kelvin's theorem, since the total circulation round a contour enclosing *both* wings remains zero!).

There is immense scope for research in this field, based on further exploration of the use of the 'clap and fling' mechanism and other specialised unsteady aerodynamic effects by flying animals. It will be of interest to determine how widespread is the use of the mechanism by insects so small that they encounter low-Reynolds-number problems. A quite different question is whether the mechanism has been used at all by much larger animals, operating at substantial Reynolds numbers. For example, butterflies (suborder Papilionoidae of the Lepidoptera) hold their wings 'clapped together' behind their back when resting, and appear to use a 'fling' mechanism, followed by a second 'fling' from a position with the wings clapped together ventrally, to facilitate rapid generation of the lift needed for take-off. This and many other exceptional features of the flight of butterflies would repay aerodynamic analysis.

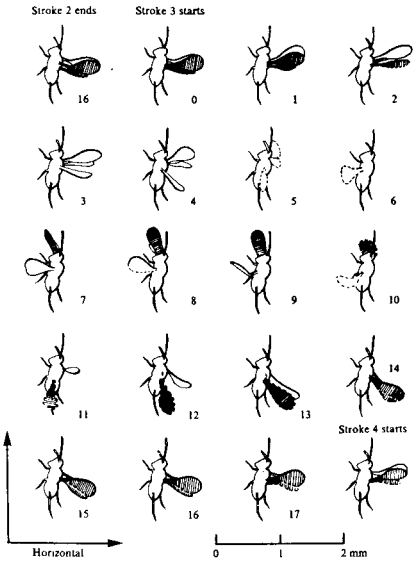

Figure 56.
Tracings from a slow-motion film, at 7150 frames per second, of a hovering specimen of Encarsia formosa (Weis-Fogh 1973).

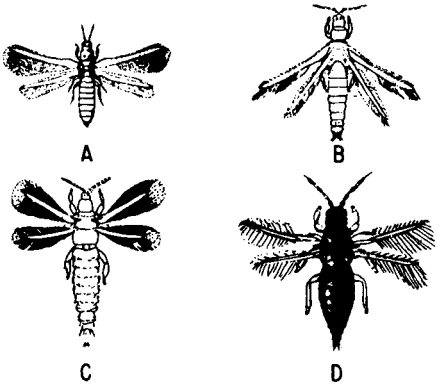

Figure 57.
Selected species of Thysanoptera (Borror & DeLong 1964).

I shall conclude by mentioning just two other orders of insects whose hovering flight would be specially worth studying in detail. The Odonata exhibit quite exeptional modes of hovering flight, with the body horizontal. It would be of great interest to analyse the complicated combinations of wing motions involved.

Finally, the Thysanoptera appear to have penetrated into regions of still lower Reynolds number (<10) than those discussed above, in association with a quite exceptional wing morphology (figure 57), almost suggestive of ciliary arrangements for aquatic motions at low Reynolds number. It will be a challenging problem to study by experiment and analysis what are the special movements by which these 'thrips' or 'fringe-winged' insects are enabled, at such very low Reynolds numbers, to support their bodies in the air.

Acknowledgement

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Bibliography

Allen, G. M. 1940 *Bats*. Harvard Univ. Press.

Borror, D. J. & De Long, D. M. 1964 *Introduction to the study of insects*. New York: Holt, Rinehart & Winston.

Brown, R. H. J. 1948 The flight of birds. *J. exp. Biol.* 25, 322–333.

Brown, R. H. J. 1953 The flight of birds. II. Wing function in relation to flight speed. *J. exp. Biol.* 30, 90–103.

Chapman, R. F. 1969 *The insects: structure and function*. London: English Universities Press.

Dorst, J. 1962 *The migrations of birds*. London: Heinemann.

Eisentraut, M. 1936 Beitrag zur Mechanik des Fledermausfluges. *Zeit. wissen. Zool.* 148, 159–188.

Faust, R. 1952 Untersuchen zum Halterenproblem. *Zool. Jahrb., Allg. Zool. Physiol.* 63, 325–366.

Fisher, M. L. 1950 *The Albatross of Midway Island*. Southern Illinois Univ. Press.

Fox, R. M. & Fox, J. W. 1964 *Introduction to comparative entomology*. New York: Reinhold.

Gray, J. 1968 *Animal Locomotion*. London: Weidenfeld & Nicolson.

Greenewalt, C. H. 1962 Dimensional relationships for flying animals. *Smithsonian Misc. Coll.* 144, no. 2, 46 pp.

Hankin, E. H. 1913 *Animal Flight*. London: Iliffe & Sons.

Hanzák, J. 1967 *Pictorial Encyclopedia of Birds*. London: Paul Hamlyn.

Hocking, B. 1951 The intrinsic range and speed of flight of insects. *Trans. Roy. Entomol. Soc. London* 104, 223–345.

Horton-Smith, C. 1938 *The flight of birds*. London: H. F. & G. Witherby, Ltd.

Jensen, M. & Weis-Fogh, T. 1962 Biology and physics of locust flight. V. *Phil. Trans. Roy. Soc. B*, 245, 137–169.

Johnson, C. G. 1969 *Migration and dispersal of insects by flight*. London: Methuen.

Kármán, T. 1954 *Aerodynamics*. Cornell Univ. Press.

Lack, D. 1956 *Swifts in a tower*. London: Methuen.

Lighthill, M. J. 1969 Hydromechanics of aquatic animal propulsion. *Ann. Rev. Fluid. Mech.* 1, 413–446.

Lighthill, M. J. 1970 Aquatic animal propulsion of high hydromechanical efficiency. *J. Fluid Mech.* 44, 265–301.

Lighthill, M. J. 1973a Aquatic animal locomotion. In *Proc. 13th Int. Congr. Theor. Appl. Mech.* (Ed. Becker, E. and Mikhailov, G. K.) pp. 29–46. Berlin: Springer.

Lighthill, M. J. 1973b On the Weis-Fogh mechanism of lift generation. *J. Fluid Mech.* 60, 1–17.

Marshall, N. B. 1965 *The life of fishes*. London: Weidenfeld & Nicolson.

McGillivray, W. 1840 *British Birds*, vol. 3. London: Scott, Webster & Geary.

Meinertzhagen, R. 1955 The speed and altitude of bird flight (with notes on other animals). *Ibis* 97, 81–117.

Mittelstaedt, H. 1950 Physiologie des Gleichgewichtes bei fliegenden Libellen. *Z. vergl. Physiol.* 32, 422–463.

Pennycuick, C. J. 1968 A wind-tunnel study of gliding flight in the pigeon *Columba livia*. *J. exp. Biol.* 49, 509–526.

Pennycuick, C. J. 1972 *Animal Flight*. London: Edward Arnold.

Pringle, J. W. S. 1948 The gyroscopic mechanism of the halteres of Diptera. *Phil. Trans. Roy. Soc.* B, 233, 347–384.

Pringle, J. W. S. 1957 *Insect Flight*. Cambridge Univ. Press.

Rayleigh, Lord 1883 The soaring of birds. *Nature*, 27, 534–535.

Scheithauer, W. 1967 *Hummingbirds*. London: Arthur Barker.

Smart, J. & Hughes, N.F. 1972 The insect and the plant: progressive paleoecological integration. In *Insect/Plant Relationships:* Sympos. Roy. Entomol. Soc. London, no. 6, 143–155.

Stolpe, M. & Zimmer, K. 1939 *Der Vogelflug.* Leipzig: Akademische Verlagsgesellschaft.

Thom, A. & Swart, P. 1940 The forces on an aerofoil at very low speeds. *J. Roy. Aero. Soc.* 44, 761–770.

Landsborough Thomson, A. 1964 *A New Dictionary of Birds.* London: Nelson.

Tucker, V.A. 1968 Respiratory exchange and evaporative water loss in the flying budgerigar. *J. exp. Biol.* 48, 67–87.

Weihs, D. 1973 Mechanically efficient swimming techniques for fish with negative buoyancy. *J. Marine Res.* 31, 194–209.

Weis-Fogh, T. & Jensen, M. 1956 Biology and physics of locust flight, I–IV. *Phil. Trans. Roy. Soc.* B, 239, 415–584.

Weis-Fogh, T. 1972 Energetics of hovering flight in hummingbirds and in Drosophilia. *J. exp. Biol.* 56, 79–104.

Weis-Fogh, T. 1973 Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *J. exp. Biol.* 59, 169–230.

Weis-Fogh, T. 1974 Scale, dimensions and design principles in actively flying animals. To appear in *Biol. Rev.*

Welty, J.C. 1962 *The Life of Birds.* London: W.B. Saunders.

Wimsatt, W.A. (ed.) 1970 *Biology of bats,* vol. 1. London: Academic Press.

Witherby, H.F. (ed.) 1939 *Handbook of British birds,* vol. 3. London: H.F. & G. Witherby Ltd.